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Forage Chicory: A Plant Resource for Nutrient-Rich Sites

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With 5 figures and 5 tables

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Abstract

Grazing livestock create localized nutrient patches that increase soil ionic strength (IS) and influence plant productivity. The ability of plant root systems to control ion absorption and flux to xylem, and to sequester ions reaching leaf tissue in bound, nontoxic forms are means of minimizing IS. A greenhouse experiment was conducted to determine the growth and mineral acquisition responses of forage chicory (*Cichorium intybus* L. cv. Grasslands Puna) to increasing (0.9, 4, 8, and 12 dS m^{-1}) IS in the rhizosphere obtained by additions of NaCl/$CaCl_2$ (1 : 1 M ratio). Plants were harvested four times after planting (20, 27, 34 and 41 d) to identify responses as a function of time. Increased accumulation and localization of Na in roots in comparison to shoots suggested that chicory restricted Na transport to shoots, and that insoluble Na in tissues increased with increasing IS. Soluble cations in shoots were about 50 % of total cations, irrespective of rhizosphere IS and Na uptake. Differences in the cation:anion ratio could not be accounted for by organic acid concentrations in chicory, but substantial accumulation of nonstructural carbohydrates as fructans in roots could contribute to charge balance. Our results demonstrate that forage chicory has moderate tolerance to IS, suggesting that it might be a useful species for sites with potential for IS. Chicory growth would probably be sustained under IS conditions, and the resultant vigorous growth and accumulation of mineral nutrients in shoots would contribute to acceptable nutritive value for grazing livestock. Plants capable of growing in and acquiring nutrients from nutrient-laden patches in the sward would help minimize erosion and nutrient transport, with positive benefits for water and soil quality.

Key words: chicory — ionic strength — nutritive value — dry matter yield — mineral content

Introduction

Grazing livestock deposit manure and create in pastures localized patches of nutrients that are, in part, determined, by grazing behaviour, grazing management and landscape features (Wilkinson et al. 1989). Nutrients accumulate at or near the soil surface when manure from confinement feeding operations are applied to or stored on agricultural land. These concentrated nutrient patches create soil conditions, such as increased ionic strength (IS) or excessive nutrients (Whitehead 1995), that influence plant growth, persistence and nutritive value (Grattan and Grieve 1994, Eschie and Rodriguez 1999, Mer et al. 2000) and increase the potential for nutrient runoff. 60 to 90 % of herbage nutrients ingested by grazing livestock are returned to pasture in urine and dung, covering about 30–40 % of a pasture annually (Haynes and Williams 1993).

Phosphorus, Ca and Mg are returned as faeces (80–99 %), whereas N, Na and Cl occur in roughly equal amounts in urine and faeces. About 60–80 % of the K excreted by grazing livestock is returned in urine (Haynes and Williams 1993). Nutrients in faeces and urine could contribute to increased IS in localized patches in the pasture. For example, IS increased under grazing in both lowland and upland situations from 1.03 and 0.83–3.88 and 6.85 dS m^{-1}, respectively (Chaneton and Lavado 1996). When precipitation is limited, nutrients accumulate at the surface of the rhizosphere. Short-duration drought and high stocking densities in humid regions might create conditions conducive to nutrient accumulation and short-term IS stress.

Chicory (*Cichorium intybus* L.) grows under a range of marginal soil conditions, being common along roadsides and in abandoned fields, and has well-documented forage production and nutritive value qualities for well-managed conditions (Jung et al. 1996, Volesky 1996, Collins and McCoy 1997, Belesky et al. 2000). Herbage production increased with increasing nitrogen application (Clark et al.

1990, Collins and McCoy 1997, Belesky et al. 2000). Nitrogen application increased crude protein and soluble NO_3-N, especially early in the growing season (Belesky et al. 2000). Similar responses were observed for chicory produced for human consumption (Santamaria et al. 1998). Concentrations of macronutrients (K, Ca, Mg, P and S) were high in chicory herbage (Belesky et al. 2001), suggesting that chicory is a vigorous accumulator of mineral nutrients. Plant mineral composition is influenced by the source of IS (Grattan and Grieve 1994, Marschner 1986) as is the nutritive value of chicory (Neel et al. 2002).

High IS shifted the balance of species growing in highway medians from grasses to native forbs (St. Arnaud and Vincent 1988), suggesting that genetically improved forbs could be valuable renovation or site remediation tools for IS stress situations. Chicory originated in the Mediterranean region (Vavilov 1992) where water and IS stress conditions are widespread. The plant also commonly grows along highway verges in the northern US where de-icing salts are used. However, information on the tolerance of forage chicory to IS in the rhizosphere is lacking. Producers need IS-tolerant forage plants for use as bioremediators on nutrient-laden sites, such as old feedlots or compost storage sites, as well as in mixed species pastures where localized zones of IS stress occur. We conducted greenhouse experiments with chicory to determine if the growth and mineral uptake of forage chicory was influenced by IS in the rhizosphere and consider responses in the light of potential uses for chicory as a forage and bioremediation tool.

Materials and Methods

Growth conditions

Forage chicory, cv. Grasslands Puna, was sown into 3.2 L capacity plastic pots containing 1.4 kg of potting mix (Premier Horticulture Inc. Red Hill, PA*). Plants were grown in a greenhouse (average day/night temperatures were set to 25/18 °C, relative humidity to 50 %) beginning June 5 2000, watered daily with deionized water, and thinned to 7 seedlings pot^{-1} before treatments were imposed. Treatments were irrigated with four solutions of increasing ionic strength (IS) (0.9, 4, 8 and 12 dS m^{-1}), with each treatment replicated 16 times for a total of 64 pots. The composition of the nutrient solution was: 1.5 mM $Ca(NO_3)_2$; 1 mM NH_4NO_3; 0.5 mM KH_2PO_4; 3 mM KNO_3; 0.5 mM $MgSO_4$; and micronutrients supplied according to the Long Ashton formula (Hewitt 1966). Projected IS was obtained by addition of (0, 11.5, 29.5 and 51.0 ml) of $NaCl/CaCl_2$ solution (1 : 1 M:*M*) in order to obtain the target IS of 0.9, 4, 8 and 12 dS m^{-1} in solutions. The pH of all nutrient solutions was adjusted to 6.0 using 1 M NaOH. Treatments were introduced gradually over 3 days (one-third IS each day) to prevent osmotic shock to the plants. Free-draining pots were watered twice daily throughout the experiment (41 days) with excess nutrient solution (300–500 ml) corresponding to a particular treatment.

Sampling and analysis

Four replicate pots from each treatment were harvested at 20, 27, 34 and 41 days after planting. Shoots were severed from roots and the lower stalks rinsed with deionized water and blotted dry before leaf area measurement (Decagon Devices Inc. Agimage Analysis, Pullman, WA, USA). Roots were removed from the potting mix and washed thoroughly to remove the potting mix. Shoots and roots were oven-dried at 65 °C for a minimum of 48 h and dry weights recorded.

Shoots and roots were ground to pass a 0.5 mm screen and kept in sealed plastic bags for subsequent total and soluble mineral analysis. Tissues were microwave-digested (Kingston and Jassie 1988) and brought to a final volume of 10 ml with distilled, deionized water. Solutions were filtered and stored in plastic tubes at 5 °C for ICP (Jobin Yvon Model JY 46P ICP, Longjumeau, France) mineral analysis. Total N in shoot and root tissues was determined using a Carlo Erba analyzer (EA 1108 CHNSO, Milan, Italy).

Soluble anions (NO_3^-, Cl^-, F^-, SO_4^{-2}, $H_2PO_4^-$) and cations (NH_4^+, K^+, Na^+, Ca^{+2}, Mg^{+2}) were determined by extracting 50–100 mg ground shoot or root tissue with 10 ml of deionized water. Vials of samples were immersed in a hot water bath (65 °C) for 1 h. Extracts were filtered through no. 1 Whatman filter paper and kept at −10 °C until analysis (Dionex DX 500 ion chromatography, AS 14 4 mm anion column and CS 14 4 mm cation column).

Ash alkalinity (Van Tuil et al. 1964) was determined by ashing subsamples (250–500 mg) of dried, ground tissues in porcelain crucibles at 500 °C for 6 h. The cool ash was dissolved in 10 ml of 1 M standardized HCl and titrated to pH 7.0 using standard 1 M NaOH. The difference in cmol kg^{-1} between the two standard solutions represents alkalinity of the ash.

Nitrate reductase activity (NRA) was determined at 41 days after planting (method adapted from Klepper et al. 1971). Thirty, 6 mm diameter leaf discs, totaling 0.5 g fresh mass, were collected randomly from plants in each pot. Discs were placed in 25 ml of KH_2PO_4 buffer (0.1 M, pH 7.5, containing 1 % (v/v) 1-propanol) in dark flasks. Samples were vacuum infiltrated for 1 min, flushed with N_2 gas for 30 s, and incubated in a water bath at 25 °C. Samples of 0.5 ml were analyzed at intervals for nitrite concentration (Snell and Snell 1949). NRA was estimated from the slope of increasing nitrite in solution as a function of time. Potential NRA was determined by adding 100 mM of KNO_3 to the assay buffer.

Collection of xylem sap

A hydroponic experiment was carried out in growth chambers (16 h photoperiod; 25/20 °C day/night; 60 %

relative humidity) to generate plants for xylem exudate sampling. Seedlings of Puna (8 days old) were transferred into 1 L pots containing nutrient solutions (pH 6.0), with one seedling per pot. Nutrient solutions and IS treatments were identical to those reported earlier for the experiment conducted in the potting mix. Solutions were replenished daily with freshly prepared solutions according to treatment, and were aerated continuously throughout the experiment (21 days). At harvest, shoots were separated from the roots and xylem sap was collected for a period of 5 min from each plant using a pressure bomb 0.2–0.4 mPa (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) at 1.4–2.8 Pa. Exudate samples were bulked prior to ion exchange chromatography analysis for NO_3^-, Cl^-, SO_4^{-2}, $H_2PO_4^-$, NH_4^+, K^+, Na^+, Ca^{+2} and Mg^{+2}.

Calculations and statistical analysis

Specific accumulation rates for macro- and micronutrient elements (SAcR, μg nutrient g^{-1} DM d^{-1}) were calculated as:

$$SAcR = (N4 - N1)/(T4 - T1) \times \ln(W4/W1)/(W4 - W1)$$

where N4 and N1 are the macro- and micronutrient content of shoots, W4 and W1 are the shoot dry matter, and T4 and T1 are the time (days(d)) for plants at harvest dates 4 and 1 (Williams 1946).

Data were analyzed using general linear models of the analysis of variance procedure (SAS Institute 1999). Sources of variation were IS, harvest date (HD) and the interactions of IS rate and HD. Single degree-of-freedom orthogonal polynomial contrasts were calculated for the influence of IS on growth, mineral nutrient concentrations and SAcR. Differences among significant treatment effects for each variable were compared by mean separation procedures and the calculation of least significant difference (LSD) at 5 %.

Results and Discussion

Dry matter production and allocation

Plant IS tolerance is determined by relating growth with differing IS to a very low (0.9 dS m^{-1}) IS control. A 50 % reduction in the mass of the structure of interest is used as the threshold level for plant tolerance to salinity and provides the basis for a relative tolerance scale (Francois and Maas 1999). Chicory growth was unaffected by up to 4 dS m^{-1} IS, making chicory moderately tolerant of salinity stress. At IS greater than 4 dS m^{-1}, mass accumulation was significantly less than that achieved at 0.9 dS m^{-1}. For example, shoot mass was 49 % less at 41 days after planting compared to 0.9–12 dS m^{-1} IS plants. Shoot was greater than root mass in the first 6 week of growth, regardless of IS. Shoot and root mass increased with successive HD (Table 1) and did so more rapidly at 0.9 dS m^{-1}than at greater IS (Fig. 1). The shoot mass was unaffected by IS up to 27 days after planting. Differences in root mass were not apparent until 41 days after planting. Root growth was slow and similar among IS treatments up to day 34. Root mass increased 400 % at 0.9 dS m^{-1}, and about 150 % at 12 dS m^{-1}, between 34 and 42 days after planting (Fig. 1).

Table 1: Analysis of variance for rhizosphere ionic strength (IS), harvest date (HD), and the interaction of IS and HD on shoot and root dry matter (DM), shoot:root ratio, and leaf area. Also presented are single-degree-of-freedom orthogonal polynomial contrasts for the influence of IS on each parameter

Effect	d.f.	Shoot DM	Root DM	Shoot:root ratio	Leaf area
IS	3	***	***	***	***
Linear	1	***	**	**	NS
Quadratic	1	***	***	***	***
HD	3	***	***	***	***
IS × HD	9	***	***	NS	***

** Significant at $P > 0.1$; *** significant at $P < 0.001$; NS, not significant.

Morphological adjustments to environmental conditions are often adaptive measures that enhance plant fitness (Sultan 2000). Allocation of photosynthate among structures can change, improving capture of resources, while toxicities can disrupt physiological processes and production efficiencies. The relative changes in shoot and root growth of Puna chicory led to a decreased shoot:-root ratio (Fig. 1). Changing allocation of photosynthate to root rather than shoot occurred irrespective of IS level (Fig. 1). The shift to root mass accumulation around day 34 corresponded to the developmental stages of chicory described by Ameziane et al. (1995), which leads to fructan accumulation as the plants mature. The decrease in shoot:root ratio was greater in control and 4 dS m^{-1} than in IS 8 and 12 dS m^{-1} treatments. After 34 days of growth, the leaf area was at least at 12 dS m^{-1} and greatest at 0.9 dS m^{-1} (Fig. 1). Reduction in leaf area occurred because the plants had fewer leaves and was not due to reduced leaf expansion (data not shown).

Macronutrients

Concentrations of macronutrients, with the exception of K, were influenced by rhizosphere IS (Table 2). A summary of trends in macronutrients follows, while the actual data is not shown.

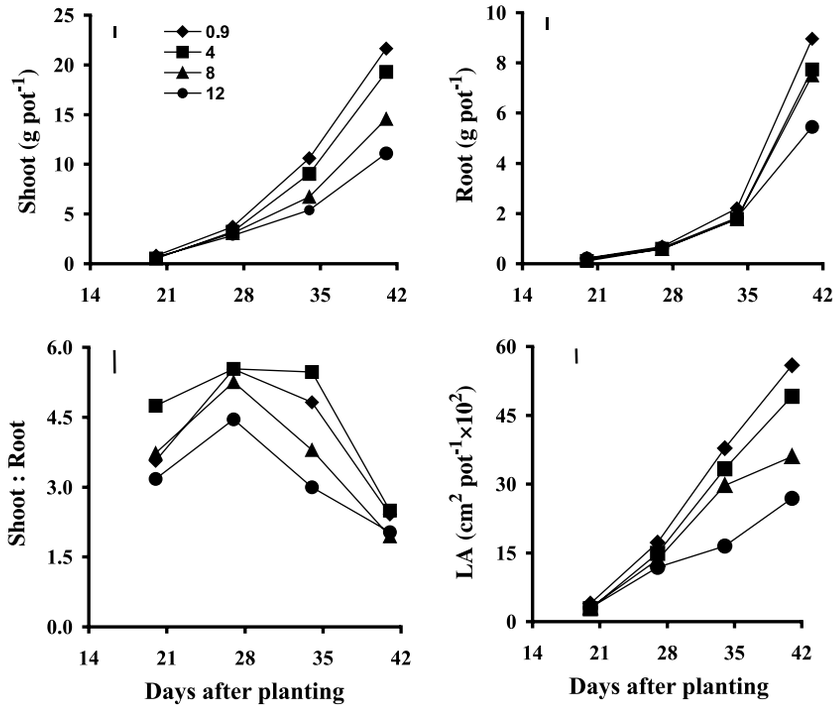

Fig. 1: Effect of ionic strength (IS) on shoot and root DM, leaf area, and shoot: root ratio of Puna chicory, as influenced by ionic strength (IS) of 0.9, 4, 8 or 12 dS m^{-1}. Vertical bar is LSD at P = 0.05

Table 2: Analysis of variance for rhizosphere ionic strength (IS), harvest date (HD), and the interaction of IS and HD on macro- and micronutrient concentrations in shoot dry matter (DM). Also presented are single degree-of-freedom orthogonal polynomial contrasts for the influence of IS

Effect	d.f.	N	K	Ca	Mg	P	S	Na	Cl^-
IS	3	*	*	***	**	**	***	***	***
Linear	1	NS	NS	NS	NS	NS	***	NS	***
Quadratic	1	**	NS	***	***	***	**	***	***
HD	3	***	***	***	***	***	***	NS	*
IS × HD	9	***	*	NS	NS	**	**	NS	***
		NO_3^-	SO_4^-	Zn	Cu	Mn	Fe	B	Mo
IS	3	***	***	***	*	***	NS	NS	NS
Linear	1	***	***	NS	NS	***	NS	NS	NS
Quadratic	1	***	***	***	*	***	NS	*	NS
HD	3	***	***	**	***	***	***	NS	***
IS × HD	9	***	***	***	**	***	NS	**	NS

* P < 0.05; ** P < 0.01; *** P < 0.001; NS, Not significant.

Nitrogen concentrations ranged from 55 to 65 mg g^{-1} DM at d 20, and were greater in control than in IS (4 through 12 dS m^{-1}) plants. Concentrations were less in control plants than in IS plants by the end of the experiment.

Potassium concentrations were greatest in control plants at day 20 and declined thereafter so that the IS plant K was greater than that of control plants by day 41. Phosphorus concentrations in shoots declined during the course of the experiment and were not affected by increasing IS. Sulphur and Mg concentrations were greater in control than in IS stressed plants after 27 days of growth. Concentrations of S and Mg declined during 41 days of growth and were greater in IS than in control plants. The IS plants had greater S and Mg concentrations than those (> 2 mg g^{-1} DM) considered critical for normal plant growth. Calcium concentrations did not change with time and were greater with increased IS.

Chicory was moderately tolerant to IS but the slight depression in growth with increasing IS could not be explained by N, S, P, Ca, Mg and K

Table 3: Specific accumulation rates (SAcR) of macro and micronutrients in shoots of chicory as they were affected by ionic strength (IS) between harvests 1 and 4 (21 days) with single degree-of-freedom orthogonal polynomial contrasts

Macronutrients	N	P	S	Ca	Mg	Na	K
IS (dS m^{-1})			(SAcR, mg g^{-1} DM d^{-1})				
0.9	4.38	0.89	0.55	2.67	0.47	1.01	14.14
4	5.45	0.92	0.39	3.83	0.49	4.70	20.02
8	5.39	0.96	0.41	3.96	0.33	5.06	21.54
12	5.27	0.82	0.40	4.40	0.24	6.57	17.18
				P > *F*			
IS	*	NS	***	***	***	***	**
Linear	NS	NS	***	***	NS	***	***
Quadratic	**	NS	**	***	***	***	NS
Micronutrients	B	Mo	Zn	Cu	Mn	Fe	
IS (dS m^{-1})			(SAcR, μg g^{-1} DM d^{-1})				
0.9	5.52	0.45	5.17	0.66	8.33	12.51	
4	4.96	0.53	7.08	0.99	16.32	14.61	
8	4.35	0.37	9.81	1.04	19.80	13.07	
12	4.07	0.06	10.51	1.50	21.42	11.14	
IS	*	*	***	**	***	NS	
Linear	NS	NS	NS	NS	***	NS	
Quadratic	***	*	***	**	***	NS	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, Not significant.

concentrations or the accumulation in shoots (Table 3). Increased Na concentrations corresponded with decreased Ca. Reduced growth could arise from greater amounts of Na and Cl in shoots, with concentrations of each reaching as much as 6 % at IS 12 dS m^{-1} (Figs. 2 and 3). While the leaves of the IS plants were a darker green color, no toxicity symptoms associated with high concentrations of Na and Cl or K were evident.

Concentrations of Na and Cl were high and proportional to IS. Na concentrations in shoots changed little during 41days of growth (Fig. 2), while Cl decreased in control and increased or remained the same depending on IS in IS plants (Fig. 3). Soluble Na (ion chromatography) was less than total Na (digested plant tissues). The average soluble Na increased as IS decreased (Fig. 2). Chicory restricts Na translocation to shoots since there was greater total and soluble Na in the roots compared to the shoots (Table 4). Soluble K:Na ratios in shoots and roots were greatest at 0.9 dS m^{-1}, decreased with increasing IS, and were greater in shoots in comparison to roots (Table 4).

The increase in soluble Na and flux to shoots did not inhibit K uptake, leading to a smaller K:Na ratio in shoots and roots as IS increased (Table 4). The greater K:Na ratio in shoots in comparison to roots at all IS levels suggests greater K relative to

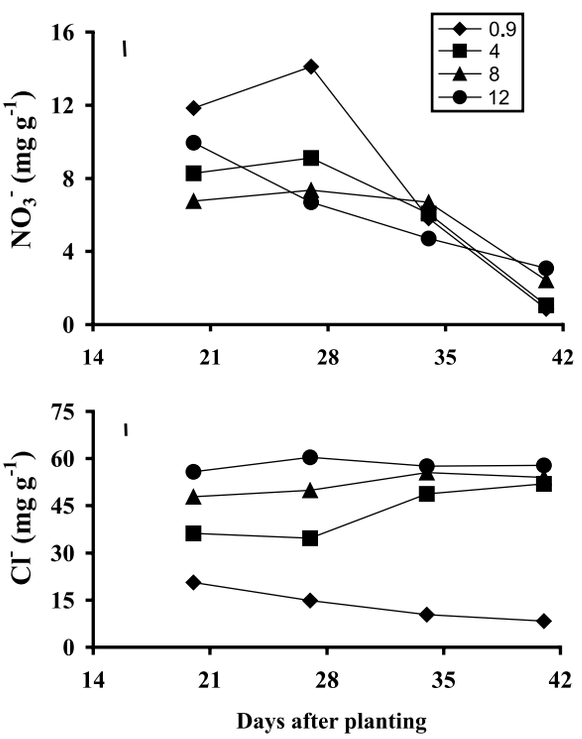

Fig. 2: Total Na and soluble Na as a fraction of total Na in shoots of Puna chicory as influenced by the ionic strength (IS) of 0.9, 4, 8 or 12 dS m^{-1}. Vertical bar is LSD at $P = 0.05$

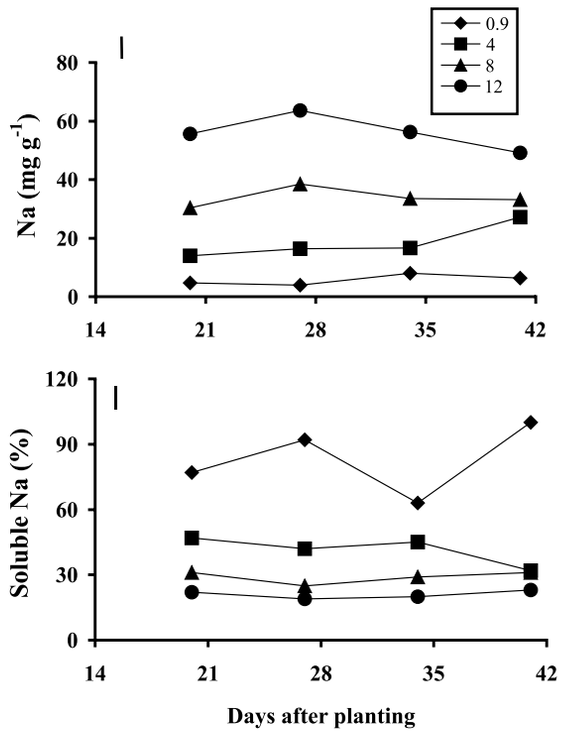

Fig. 3: Soluble NO_3^-, Cl^- and SO_4^{-2} in shoots of Puna chicory as influenced by ionic strength (IS) of 0.9, 4, 8 or 12 dS m^{-1}. Vertical bar is LSD at P = 0.05

Na transport (Table 4). The amount of soluble Na in leaves decreased with increasing Na concentrations, so K:Na ratio reflects not only transport properties of Na and K from roots, but also transport to and localization in shoots (see Flowers and Hajibagheri 2001).

The net sum uptake of cations (ΣK + Ca + Mg + Na) increased as IS increased (Table 4), with only small portions of total cation being soluble and contributing to cell osmotic pressure. The sum of soluble cation (measured in water extract of shoot tissues) as a percentage of total cation (acid-digested shoot tissue) was essentially constant in the shoot throughout the experiment, averaging about 50 % irrespective of ionic strength. The sum of soluble cations declined in roots from means of 60–85 % at day 20 to about 20 % by day 41 (Fig. 4).

Cation:anion (C:A) ratio was expressed as soluble cations or anions extracted from tissues, assuming that bound or sorbed cations would not influence regulation of cytoplasmic pH. The uptake of both cations and anions increased by increasing IS in nutrient solution; the increase being proportionally greater in anion than cation resulted in decreased C:A ratios (Table 4). The C:A ratio could be compensated for by organic acids (see

Table 4: Cation (C^+), anion (A^-), organic acid concentrations, soluble K, Na, K:Na ratio, and contribution of soluble Na to total cation in shoot and root dry matter of chicory growing at different ionic strength (IS), with single degree-of-freedom orthogonal polynomial contrasts

	C^+†	A^-‡	C – A	Organic acids	Soluble K	Soluble Na	K:Na	% Na of C^+
					meq g^{-1} Shoot DM			
IS (dS m^{-1})								
0.9	2.50	0.75	1.75	1.71	1.83	0.20	10.06	8.30
4	2.81	1.46	1.36	0.71	1.95	0.32	6.25	11.58
8	3.08	1.69	1.39	0.38	2.00	0.42	4.78	13.70
12	3.21	1.85	1.35	0.13	1.86	0.51	3.67	15.99
IS	***	***	***	***	**	***	***	***
Linear	***	***	***	***	***	***	***	***
Quadratic	***	***	**	***	NS	***	***	***
					meq g^{-1} Root DM			
IS (dS m^{-1})								
0.9	1.62	0.36	1.26	0.96	0.98	0.40	2.92	25.02
4	1.88	0.74	1.14	0.32	1.19	0.43	2.98	23.13
8	1.88	0.96	0.92	– 0.13	1.08	0.55	2.09	30.94
12	1.87	1.03	0.85	– 0.26	1.02	0.55	1.91	30.12
IS	***	***	***	***	***	***	***	***
Linear	***	***	NS	***	***	NS	NS	NS
Quadratic	***	***	***	***	NS	***	***	***

* P < 0.05; ** P < 0.01; *** P < 0.001; NS, Not significant.
† $C^+ = \Sigma (K^+ + Ca^{++} + Mg^{++} + Na^+ + NH_4 - N)$; ‡ $A^- = \Sigma (NO_3 - N + H_2PO_4^- + SO_4^- + Cl^- + F^-)$.

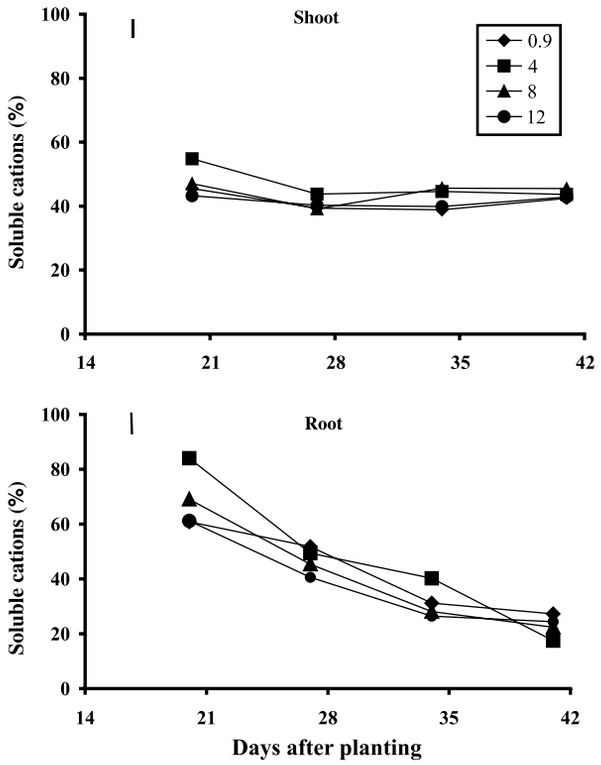

Fig. 4: Soluble cation expressed as a fraction of the total in shoot and root DM of Puna chicory as influenced by ionic strength (IS) of 0.9, 4, 8 or 12 dS m^{-1}. Vertical bar is LSD at P = 0.05

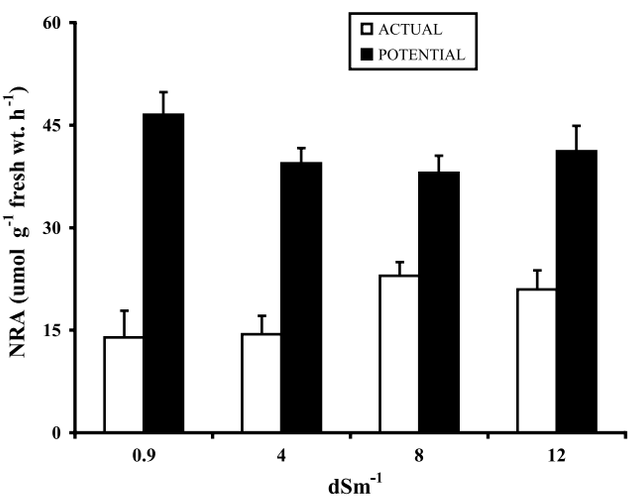

Fig. 5: Actual and potential NRA in shoots (μmol NO3 g^{-1}, shoot fresh weight h^{-1}) of Grasslands Puna as a function of ionic strength (IS) of 0.9, 4, 8 or 12 dS m^{-1}. Standard error of the mean shown for each bar

Kirkby and Knight 1977). Trends in organic acid anions were similar to C:A ratios that decreased with increasing IS (Table 4) and agreed with reports by Sagi et al. (1997), Sagi et al. (1998). In addition, forage chicory roots accumulated inulins (nonstructural carbohydrates with carboxylic functional groups) as IS increased (data not shown). About 60 % of the root mass was nonstructural carbohydrate by day 41, and may have contributed to the ionic balance.

Nitrate in shoots decreased with time and were very high at early stages of chicory growth, regardless of IS (Fig. 3). Concentrations were significantly greater at IS 0.9 dS m^{-1}than at IS 4 through 12 dS m^{-1} up to 27 days after planting, and declined slightly thereafter. Salinity influenced N uptake and metabolism in a number of plant species (Grattan and Grieve 1994, Thomas and Langdale 1980, Kafkafi et al. 1982, Martinez et al. 1994). Nitrate uptake and concentrations declined and were followed by a decrease in the NRA in the shoots of plants grown in saline conditions (Albassam 2001; Botella et al. 1997). Greater NRA in IS plants (Fig. 5) corresponded to greater concentrations of NO_3 in shoots (Fig. 3). Salinity did not seem to influence NO_3 metabolism in Puna chicory since potential NRA was not affected when NO_3 supply was unlimited (Fig. 5). Our data for chicory agrees with observations also made for *Ricinus communis* L. (Peuke et al. 1996) and *Lolium multiflorum* Lam. (Sagi et al. 1998). Xylem exudate samples from chicory (Table 5) shows that more NO_3 is transported to the shoots of IS in comparison to the control plants, and agrees with the results for *R. communis* L. (Peuke et al. 1996). On the other hand, Albassam (2001), Botella et al. (1997) and Omarov et al. (1998) reported decreased NRA in salt-stressed millet (*Panicum* sp.), barley (*Hordeum vulgare* L) and castor beans.

Micronutrients

Micronutrient concentrations, with the exception of B, Fe or Mo, were affected by IS but not HD (Table 2). Increasing IS increased concentrations of Zn, Cu and Mn in the shoot of chicory plants, with the greatest concentrations at IS 12 dS m^{-1} (data not shown). Micronutrient concentrations changed within a small range during the experiment irrespective of IS, while concentrations decreased as the experiment progressed in control plants.

Specific accumulation rate

Nutrient uptake and translocation to shoots expressed as SAcR, accounts for the efficiency with which nutrients are transported to and are accumulated in shoots. Increasing IS influenced SAcR in the shoots (Table 3). Plants exposed to IS

Table 5: Cation–anion balance of xylem exudates from Puna chicory as influenced by ionic strength (IS) in the rhizosphere. Values in parentheses are contribution (%) of a given nutrient to total cation or anion

	Cations					Anions				
	K^+	Ca^{2+}	Mg^{2+}	Na^+	Total	NO_3^-	S†	P†	Cl^-	Total
IS dS m^{-1}	meq l^{-1}									
0.9	21.37 (66)	7.35 (23)	3.37 (10)	0.35 (1)	32.43	1.66 (28)	0.72 (12)	0.62 (10)	3.02 (50)	6.02
4.0	51.03 (70)	12.34 (17)	5.24 (7)	4.42 (6)	73.04	3.76 (12)	0.97 (3)	1.11 (4)	25.74 (82)	31.58
8.0	64.63 (65)	11.50 (12)	12.60 (13)	10.96 (11)	99.69	2.33 (5)	0.54 (1)	1.18 (2)	46.76 (92)	50.81
12.0	308.77 (65)	53.61 (11)	54.03 (11)	60.34 (13)	476.74	2.55 (1)	0.28 (< 1)	1.28 (< 1)	195.02 (98)	199.13

† S and P assigned charges as 2 and 1, respectively.

accumulated more N, Ca, Na and K, while the reverse occurred for S and Mg (Table 3). Phosphorus accumulation was unaffected. The SAcR were greater for Na and Ca as these ions increased in nutrient solutions as IS increased. High concentrations of Ca limited Mg uptake (SAcR value decreased by 50 % at IS 12 dS m^{-1}), a phenomenon often observed in plants growing on calcareous soils (Marschner 1986). Nitrogen SAcR increased by 25 % from IS 0.9–4 dS m^{-1} and remained almost unchanged thereafter. Xylem exudate data confirmed greater transport of ions to shoots (Table 3). The SAcR for Zn, Cu and Mn doubled, whereas it decreased for B and Mo as IS increased. Micronutrients, such as Zn, Cu, Mn and Fe, often increase with stress (e.g. nutrient and water deficit) and can be related to changes in organic compounds accumulated by roots in order to maintain osmotic balance (Marschner 1986). In our study, organic acid anions did not increase with increasing IS and, therefore, do not help explain the enhanced concentrations and SAcR of Zn, Cu and Mn. However, reducing sugars could act as chelating agents and enhance uptake of micronutrient cations.

Our results demonstrate that forage chicory has moderate tolerance to IS (4 dSm^{-1}). The greatest salinity levels reported for pasture were 6.85 dSm^{-1} (Chaneton and Lavado 1996, Norman 1991), suggesting that Puna forage chicory might be a useful species to establish on nutrient-rich sites. Chicory growth would probably be sustained under IS conditions, and the resultant vigorous growth and accumulation of mineral nutrients in shoots would contribute to acceptable nutritive value (viz. Neel et al. 2002) for grazing livestock. Plants capable of growing in and acquiring nutrients from nutrient-laden patches in the sward would help minimize erosion and nutrient transport with positive benefits for water and soil quality.

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